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Modes of algal capture by the freshwater copepod *Diaptomus sicilis* and their relation to food-size selection[1,2]

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Abstract

High-speed motion pictures (500 frames s^{-1}) of tethered *Diaptomus sicilis* feeding in suspensions of *Chlamydomonas* spp. of three different sizes at three different concentrations (0.3, 1.0, and 3.0 mm^3 $liter^{-1}$), showed two modes of feeding: a passive mode in which algae flowed into the space between the left and right second maxillae and an active mode in which the second maxillae or second maxillae plus maxilliped made large amplitude flaps to bring in the cell. Cells ≤ 4 μm in diameter were always captured passively, and cells ≥ 6 μm were captured both actively and passively. Active captures were 18% of total captures for the medium-sized (6 μm) algae and 36% for the large (12 μm) algae. During passive captures, algae usually flowed through the space between the left and right second maxillae rather than being caught on the setules; thus, the leaky-sieve model of particle retention does not apply for passive captures by *D. sicilis*. Except for brief interruptions to actively capture a large alga nearby, the second maxillae of *D. sicilis* oscillated continuously at low amplitude at all times during feeding, in marked contrast to the marine copepods *Eucalanus* and *Paracalanus* that vibrated their second maxillae to enhance capture in monocultures of small algae but not large algae. These observations explained both the shape of the curve of selectivity vs. particle size for *D. sicilis* and its relative invariance. Analyses of feeding mechanisms and the water currents around *Diaptomus* showed that, in contrast to *Eucalanus* and *Paracalanus*, *Diaptomus* is specialized for capturing small particles, which may be a more important food in freshwater than in marine environments.

The first high-speed motion picture films (500 frames s^{-1}) of copepod feeding showed that the marine calanoid copepod *Eucalanus crassus* sensed large algae at significant distances and used active coordinated movements of the mouthparts to bring these particles to the mouth (Alcaraz et al. 1980). Previously, herbivorous copepods were thought to be filter feeders (Cannon 1928), and selection for particles was thought in large part to be a function of the size distribution of holes in the animal's filter (e.g. Nival and Nival 1973, 1976, 1979; Boyd 1976; Frost 1977). The most developed form of the filtering model (Boyd 1976; Frost 1977; Nival and Nival 1976) argued that the cumulative frequency distribution of intersetule and intersetal distances in the second maxillae—the holes in the filter, or leaky sieve—defined the particle-size selectivity of the copepod. We suspected active capture of large particles by the freshwater calanoid copepod *Diaptomus* because the poor prediction of particle-size selection given by the leaky-sieve model in *Diaptomus sicilis* Forbes was consistent with the active capture of large particles (Vanderploeg and Ondricek-Fallscheer 1982). Hence, we wanted to see if *D. sicilis* had the same behavioral abilities as *E. crassus*.

We also wanted to observe the capture of small particles since that process had not yet been observed by high-speed cinematography. Rubenstein and Koehl (1977) and Vanderploeg and Ondricek-Fallscheer (1982) theorized that the leaky-sieve model would be a poor predictor of particle-retention efficiency even for particles captured mechanically. The classic theory of copepod feeding was developed over 50 years ago (Storch and Pfisterer 1925; Cannon 1928) from observations of *Diaptomus* and *Calanus* by techniques that were not equal to the task (e.g. Alcaraz et al. 1980; Paffenhöfer et al. 1982). Therefore we could re-examine an historically interesting problem for one of the copepod genera originally observed.

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Finally, we hoped to correlate the directly observed feeding mechanisms with the food-selectivity patterns and response of feeding rate to concentration obtained from traditional feeding experiments so that we could better understand the feeding biology of *D. sicilis* and compare it to that of marine copepods. For example, Vanderploeg (1981) suggested that the relatively invariant (bell-shaped) pattern of particle-size selection for *D. sicilis* feeding on natural seston of varying sizes was caused by the simultaneous operation of active and passive modes of feeding at all times. Such a mechanism contrasts with the observed mode-switching behavior (Price et al. 1983) of the marine copepod *Eucalanus pileatus* which shuts off its passive collection mode when given monocultures of large algae.

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Methods

All filming experiments were done during October 1981 and 1982 at Skidaway Institute of Oceanography by the methods and apparatus described by Alcaraz et al. (1980), Koehl and Strickler (1981), Paffenhöfer et al. (1982), and Price et al. (1983). Female *D. sicilis* adults (mean ± SD metasome length = 1,176 ± 29 μm; mean carbon content = 7.5 μg) were collected from the hypolimnion of Lake Michigan and shipped by air to Skidaway in insulated containers. Freshly collected animals and hypolimnetic water were shipped weekly; animals to be held for a few days before experiments were kept at 9°C, the temperature of the hypolimnion. *Diaptomus sicilis* can survive without food for several weeks at this temperature.

The three algae used as food were *Chlamydomonas oblonga* Pringsheim (UTEX 219), *Chlamydomonas proteus* Pringsheim (UTEX 216), and *Chlamydomonas* sp. (UTEX 796), having equivalent spherical diameters (ESD) ± SD of 4.0 ± 0.5, 5.8 ± 0.6, and 12.4 ± 2.3 μm; respective values of number concentration (cells ml^{-1}) per volume concentration (mm^3 $liter^{-1}$) for the three species are 22,883, 4,950, and 676. These algae film well because their intense green color provides excellent contrast with the water. Algae were kept in exponential-phase growth in unbuffered WC medium (Guillard and Lorenzen 1972) on a 12:12 LD photoperiod. Feeding suspensions were prepared by suspending the algae in 0.22-μm filtered lake water supplemented with excess N, P, and trace metals. Since filming was done at 19° ± 1°C, *D. sicilis* was acclimated by allowing the temperature of the water to increase slowly from 9°C to 19°C over a 6-h period 1–3 d before filming.

Diaptomus was tethered for filming by gluing a fine cat hair to the metasome of the animal (cf. Alcaraz et al. 1980; Paffenhöfer et al. 1982; Price et al. 1983). Most of the mortality occurred within a few hours of gluing. The survivors with the attached hairs were kept in good condition for filming by pipetting them into 500-ml bottles of algal suspension rotated on a wheel at 0.5 rpm in the dim light of a cold room maintained at 19° ± 1°C at a 12:12 LD photoperiod. Survivorship and condition of the animals used for filming was excellent. After filming, animals used were put into 25-ml vials in the cold room; almost all were alive at the end of the month.

We did two kinds of filming experiments. In the first, we kept animals in unialgal suspensions at a particular concentration, using as the feeding suspension for filming the same water in which the glued zooplankton had been feeding for 1 d; this ensured that we had healthy animals and that they were preconditioned (e.g. Donaghay and Small 1979) to the scent of the food. In the second, animals were kept in a low concentration (0.3–0.5 mm^3 $liter^{-1}$) of a species of alga for

Table 1. Mouthpart frequency ± SE(N), where N is number of individual animals filmed (for both observation of mouthpart frequency and capture mode) and mode of cell capture for different feeding conditions. Active captures made without the aid of the maxillipeds are indicated as "−mxp" and those with as "+mxp."

Algal concn (mm^3 $liter^{-1}$) and treatment	No. film sequences made	No. films with captures	No. animals exhibiting captures	Frequency (Hz)	No. of captures			Active captures (%)	Active captures made with mxp (%)
					Passive	Active −mxp	Active +mxp		
Chlamydomonas sp. (12.4-μm ESD)									
1 $\xrightarrow{1\text{ d}}$ film	28	17	8	48.11±0.95(9)	17	2	6	32.0	75
0.3–1 $\xrightarrow{1\text{ d}}$ 3 $\xrightarrow{2.5\text{ h}}$ film	11	4	2	44.66±2.79(4)	6	2	3	45.5	60
All concn	39	21	10	47.36±1.06(13)	23	4	9	36.1	69
C. proteus (5.8-μm ESD)									
0.3 $\xrightarrow{1\text{ d}}$ film	19	17	5	48.92±0.77(5)	23	6	3	28.1	33
1 $\xrightarrow{1\text{ d}}$ film	19	16	5	50.66±1.44(5)	35	4	2	14.6	40
0.3–0.5 $\xrightarrow{1\text{ d}}$ 3 $\xrightarrow{2.5\text{ h}}$ film	12	7	5	47.28±1.43(5)	30	3	2	14.3	40
All concn	50	40	15	49.15±0.74(15)	88	13	7	18.5	35
C. oblonga (4.0-μm ESD)									
0.8 $\xrightarrow{1\text{ d}}$ film	10	4	3	45.37±2.96(3)	12	0	0	0	—
0.3 $\xrightarrow{1\text{ d}}$ 3 $\xrightarrow{2.5\text{ h}}$ film	6	5	4	47.83±2.83(4)	21	0	0	0	—
All concn	16	9	7	46.77±1.95(7)	33	0	0	0	—

1 d and then placed in a high-concentration (3 mm^3 $liter^{-1}$) suspension of the same alga 2.5 h before filming. This last suspension was prepared at the same time as the low-concentration suspension and kept in a 500-ml bottle on the same rotating wheel with the low-concentration suspension containing animals. This simulated the animal's movement into a food patch and provided the maximum number of attack and ingestion events that could be expected in the first few hours in the patch (e.g. Frost 1972). Zooplankton-conditioned lake water (containing a low concentration of *Chlamydomonas* and *Diaptomus* for 1 d before filtering) was used for making up all feeding suspensions to ensure that all algae were in similar physiological condition so that they had a similar olfactory quality for *Diaptomus*.

The developed 30.5-m-long rolls of 16-mm film were analyzed frame by frame with Vanguard motion analyzer components that projected a 1-m-wide image on a white table surface. This system provided higher resolution for examining the paths of small algae than the standard Vanguard system with a projection case on which a smaller image is projected from the rear.

Results and discussion

The flow field—The frequency of mouthpart oscillation (taken from the second antenna) is quite constant over different algal concentrations and species (Table 1). The constancy of observed vibration frequency implies that the same (invariant) flow field is set up (Strickler 1982, 1984) around *D. sicilis* under all feeding conditions. Figure 1 shows the laminar (Koehl and Strickler 1981; Strickler 1982) flow field around *D. sicilis* determined by tracing paths of individual *C. proteus* (5.8-μm ESD) cells on a film. Paths are shown only for cells that did not elicit an active capture response (described below) since the asymmetric motions of the mouthparts during active capture (Koehl and Strickler 1981; Price et al. 1983) briefly distort the field. Much of the water in the flow field is directed toward the mouthparts, especially the second maxillae. The forward-directed swimming legs of *Diaptomus* appear to help direct the water into the second maxillae and to split the flow

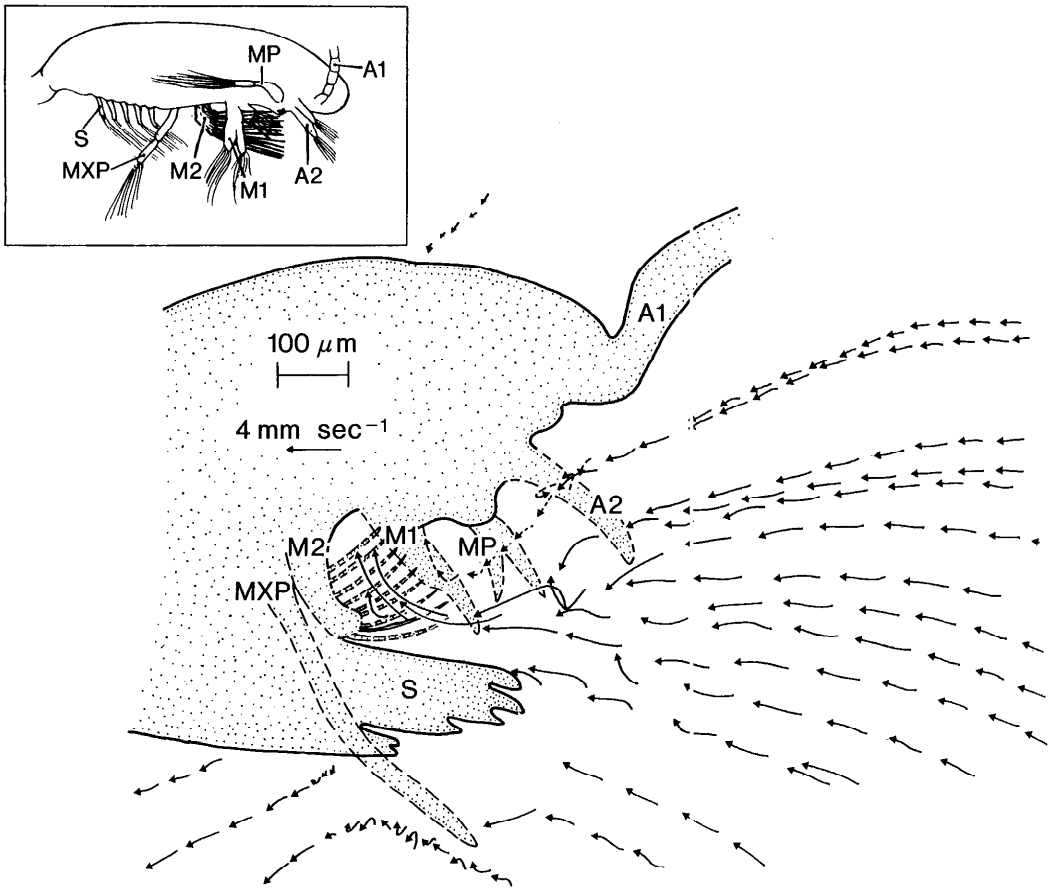

Fig. 1. Current field around a tethered *Diaptomus sicilis* seen from a nearly lateral view. Labeled body parts on drawing are: first antenna (A1), second antenna (A2), mandibular palps (MP), first maxilla (M1), second maxilla (M2), maxilliped (MXP), and swimming legs (S). The second maxilla seen on the drawing is the one farthest from the viewer (the left second maxilla), and the current vectors there are for flow between second maxillae. To simplify the drawing, 8 rather than all 16 setae of the second maxilla are shown. A dashed line around an appendage indicates it is in continuous motion when the copepod is feeding except when it is actively capturing or rejecting algae. Inset shows morphology of the marine copepod *Eucalanus pileatus* (redrawn from Koehl and Strickler 1981) for purposes of comparison. Except for the few dashed vectors near the body, all vectors were drawn by tracing paths of individual cells from a movie made of feeding in a 3 mm^3 $liter^{-1}$ suspension of *Chlamydomonas proteus*. The outlines of the moving appendages are approximations of the true appendage shape since they were never all together in perfect focus. The dashed vectors show the path a loose cluster of *Chlamydomonas* sp. took toward the mouth area on another film.

field into one component that goes toward the mouthparts and another that goes beneath the body. The invariant flow field is undoubtedly important for the animal to know the location of an alga once it detects the phycosphere of odor around the cell (Strickler 1982, 1984; Price et al. 1983). The current vectors have a wavy shape because the flow field is set up by vibrating appendages and because flow is laminar. The strong waviness in current vectors beneath the maxilliped is a dramatic visual demonstration of viscous coupling between an appendage and the surrounding water.

The second maxillae oscillated continuously at a low amplitude at all times except during active captures, rejections of particles, cleaning, or breaks (when all mouthparts stopped beating). The continuous motion of the second maxillae may be part of

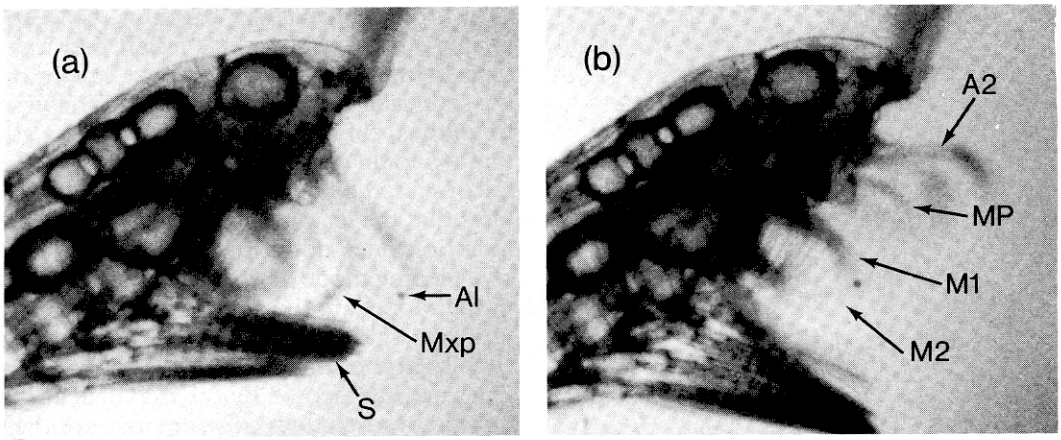

Fig. 2. Active capture of a 13-μm-diameter *Chlamydomonas* sp. cell (Al) showing use of maxilliped (Mxp), swimming legs (S), and the second maxilla (M2): a—time zero; b—10 ms later. Other labels as in Fig. 1. The large globules seen beneath the carapace are stored lipids.

the system of "wings" of the fling and clap mechanism (Strickler 1984) to bring in water between the two second maxillae. Price et al. (1983) speculated that low-amplitude oscillations of the second maxillae of *Eucalanus,* when they occurred, directed some of the usual flow of water from beneath the animal to flow between the second maxillae.

Active vs. passive captures—Price et al. (1983) observed that the marine copepods *E. pileatus* and *Paracalanus* sp. actively captured (sensu Koehl 1981; Koehl and Strickler 1981) and handled individual algal cells as small as 12 μm using the fling (Weis-Fogh 1973) and squeeze mechanism of Koehl and Strickler (1981). Continuous low-amplitude motions of the second maxillae and combing of the appendages by *E. pileatus* in suspensions of small (6 μm) cells were thought to be the feeding mode responsible for enhancing capture of small cells, although the actual captures could not be seen (Price et al. 1983). These low-amplitude motions did not occur when only large cells were present.

We were able to observe the small-particle, or passive, feeding mode in *Diaptomus* and to distinguish between it and active captures. The features typically found in an active capture can be seen in Fig. 2. In Fig. 2a the maxilliped, having responded to the presence of the alga, has moved so that its distal end, which is usually ventral to the swimming legs as in Fig. 1, has moved upward above the swimming feet, dragging the alga behind it in the viscous bond between the maxilliped and the water containing the alga. In Fig. 2b (10 ms later), the swimming legs have been pulled backward to full extent, increasing the angle (and space) between the legs and body. This appears to allow room for the second maxillae to flap open as well. Typically three flaps of the maxillae were required to capture a cell. Once the swimming legs were pulled backward, they remained there until the second maxillae stopped flapping. The swimming legs probably had to be pulled backward to allow room for the second maxillae to flap through their full range of motion. Possibly the flapping of the swimming legs also directly aided the capture (Rosenberg 1980).

During the passive captures, the continuous low amplitude vibrations of the second maxillae remain unaltered by the presence of the algae. The velocities of the particles themselves can be used to distinguish whether capture is active or passive (Fig. 3). Particles in the current field above the swimming legs (Fig. 1) can be captured passively if they are close to the medial plane of the animal. Typically a passively captured alga appears to move between the left and right second maxillae in a smoothly curved—albeit slightly wavy—path, only

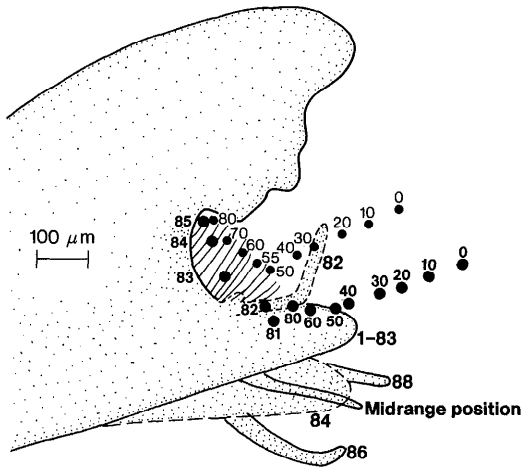

Fig. 3. Contrast between particle movement for *Diaptomus sicilis* capturing *Chlamydomonas* sp. cells actively and passively. For clarity, the first and second antennae and the first maxillae have been removed from the drawing. The setae of the right second maxilla are shown, and the particle paths are behind this maxilla, that is, between the maxillae. The bold-faced numbered path shown for the larger alga (drawn to scale) shows the position of an actively captured alga at different frames (time between two consecutive frames is 2 ms) starting from the initial point (frame zero) shown. The numbered path for the smaller alga shows the path that passively captured alga took at a different time on the same film. The positions of the maxilliped and swimming legs during the active capture cycle are shown by the large boldface numbers next to them that match up with the numbers for actively captured algae. The solid outlines of the maxilliped and the swimming feet show their normal positions. The dashed outlines of the maxilliped and swimming legs show positions they occupied only during the active capture sequence. For reference, the position of the maxilliped midway in its normal, noncapture range of motion is shown.

modestly accelerated as shown in Fig. 3. (*See also current field in Fig. 1.*) Almost all passively captured algae were displaced that way. However, a few algae took paths close to the body—like the path (dotted vectors) for the loose cluster of algal cells in Fig. 1—that led to the mouth area (between M1 and MP in Fig. 1), and there they disappeared. We presume they were ingested because individual cells in the cluster disappeared one by one in the region of the mouth. Because of the opacity of *D. sicilis* and the way the mouthparts are fitted close together between the body and swimming legs, details of the particle-handling sequence near the mouth could not be observed from any angle.

In almost all passive captures, cells appeared to travel between the left and right second maxillae and did not get caught on the setules or setae of the proximal (relative to endites) three-fourths of the setal length that we could observe. (The tips of the setae are obscured by the first maxillae.) This implies that the leaky-sieve process of particle retention does not apply even for the passive feeding mode of *D. sicilis* since implicit in the model are the assumptions that each unit area of the second maxillae participates equally in the sieving process and that particles are intercepted by the maxillae at the first point of contact (sieving) and are then scraped off and delivered to the mouth (Vanderploeg and Ondricek-Fallscheer 1982). It is possible that much of the surface of the second maxillae may function more like a funnel than like a sieve since the calculated (Fung 1969; Koehl and Strickler 1981) boundary layer thicknesses (δ)—i.e. the thicknesses of the velocity gradients—around both setules and setae are greater than half their respective spacing during passive captures (Table 2). Even for maximum spacing, which occurs near the tips, δ is still quite thick relative to half the spacing. The estimate of δ for average setal and setule spacing should be regarded as a minimum because δ was determined for the tips of the setae, where velocity is highest. If water is flowing through the setae or setules, it is probably doing so at the tips where δ is minimal and setal and setule spacing is maximal.

Our values of the Reynolds number (Re), δ, and maximal spacing between setae for *D. sicilis* are very similar to those for the large marine copepod *E. pileatus* (Koehl and Strickler 1981). At similar values of Re, flows are dynamically similar (e.g. Vogel 1981). Curiously, *E. pileatus* is able to obtain these values of Re and δ at half the beat frequency (24 Hz) of *D. sicilis*. Possibly there is a limited region of Re, δ, and setal spacing over which the passive capture mode will operate for copepods.

Combing motions of the kind used by marine copepods (Koehl and Strickler 1981; Price et al. 1983; Strickler 1984) for scraping the second maxillae were also observed for *D. sicilis* when no cells could be seen on the second maxillae. This suggests that the

Table 2. Velocity (U), Reynolds number (Re), and boundary layer thickness (δ) around setae and setules of the second maxillae during active and passive captures. An animal exhibiting typical captures was observed obliquely (from the front and side) so that maximum excursions of the second maxillae could be measured.

Structure/ kind of capture	Diam (μm)	Max U (mm s^{-1})	Re	δ* (μm)	Spacing (μm) Avg	Max
Seta						
Active	3.1†	28‡	8.7×10^{-2}	10	16	39§
Passive	3.1†	10‖	3.0×10^{-2}	18	12	22§
Setule¶						
Active	0.1†	<28‡	$<2.3\times10^{-3}$	>1.9	3†	7†
Passive	0.1†	<10‖	$<9.6\times10^{-3}$	>3.2	3†	7†

* Order of magnitude estimate (Fung 1969; Koehl and Strickler 1981).
† Data of Vanderploeg and Ondricek-Fallscheer (1982).
‡ Maximum from inward and outward motions over typical capture sequence of *Chlamydomonas* sp.
§ Average spacing between tips of four most distal setae.
‖ Average maximum velocity taken over four cycles.
¶ Results given for the setae imply that the setules are within the boundary layer of the setae; therefore, < signs are placed in front of values of maximum U for the setules. Likewise, corresponding values of Re and δ have appropriate inequality signs in front of them.

scraping may serve not only to clear occasional debris caught on the maxillae but also to remove scent that may remain in the boundary layer around the maxillae. The scent, if not removed, could interfere with detection of cells for capture.

Active capture, which always involved flaps of the swimming legs and second maxillae, resulted in a greatly accelerated motion of the alga (Fig. 3). The actively captured alga in Fig. 3 was touching or within the boundary layer of water around the swimming feet of *D. sicilis* for a long time (frames 50–80, implying 60 ms) before *D. sicilis* responded to it and accelerated it into the second maxillae. Boundary layer thickness is considerably thinner during active than during passive captures because of the higher velocity of the second maxillae during active captures (Table 2). Water flow between tips of the setae seems likely because δ is about one-fourth the distance between setae near the tips. As with passive captures, values of Re, δ, and maximal spacing between setae of *D. sicilis* during active captures are very similar to those reported for *E. pileatus* (Koehl and Strickler 1981). Again, as with the passive captures, we wonder if the fling and squeeze mechanism in calanoid copepods is restricted to a narrow region of Re, δ, and setal spacing.

Algae or fecal pellets had to be quite close to *D. sicilis* before the zooplankter would respond to their presence with active capture motions of the appendages (Fig. 4). In marked contrast, *E. pileatus* often initiated captures for cells >70 μm away (Price et al. 1983). With *D. sicilis,* cells had to almost touch the appendages or be within the boundary layer around them before the active capture response was first apparent. The maxillipeds were brought into play for those targets that the feeding currents (Fig. 1) brought near or beneath the swimming feet (Fig. 4). Although some of the algae beneath the swimming feet in Fig. 4 appear to be far from any appendage, they were very near (<25 μm) the distal portion of the maxillipeds in their normal range of motion.

Effects of algal size and concentration on modes of algal capture—To quantify the animals' use of active and passive modes of feeding, we recorded the number of each kind of capture that could be seen from an approximately lateral view of the head region focused on the medial plane of the animal like that in Figs. 1–4. This gave us a view of a relatively thin plate (small depth of field) through which we could observe algal trajectories, so that large algae were more likely to be observed than small algae. The probability of observing a capture at the lower concentrations of *C. proteus* and *Chlamydomonas* sp. during the 8-s duration of a film was unfortunately low. In order to observe many capture events at the lower concentrations, we often waited until a cell or patch of cells came into view near the animal that was creating a feeding current before filming. Thus, even within algal

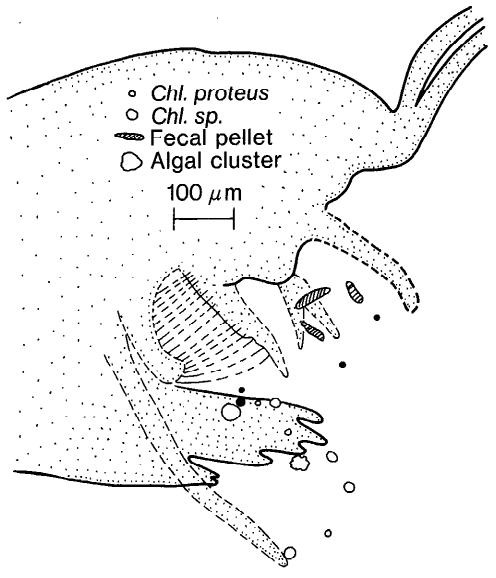

Fig. 4. Locations of different targets at time of initiation of the active capture response for those targets whose trajectories could be followed. Unshaded targets correspond to objects captured with the aid of the maxillipeds, and those shaded or hatched correspond to objects captured without the aid of the maxillipeds. All targets below the swimming legs came quite close (<25 μm) to the maxilliped within its normal range of motion.

species, nonrandom sampling prevents direct comparison of numbers of active and passive captures. To circumvent these limitations of visibility and nonrandom sampling, we compared on a percentage basis the number of active and passive captures: this also compensated for inevitable differences in quality of photographic images among films.

Our criterion for a passive capture was the observation of the alga moving between the maxillae or, in a very few cases, taking a path that led directly to the mouth area; for an active capture, the observation of flapping and of the alga being accelerated in or in the region near the second maxillae. Chi-square tests (one-tailed) for differences in probabilities (e.g. Conover 1980) determined whether the percentage of active captures differed significantly among experimental conditions. One-tailed tests were used because we thought that this percentage would decrease with decreasing algal size and increasing concentration.

As algal size decreased, the proportion of algae captured actively did decrease (Table 1). We never saw active captures of *C. oblonga,* the smallest species (4.0 μm). Averaging over all concentrations, 16% of the *C. proteus* and 36% of the *Chlamydomonas* sp. were captured actively. These three proportions are significantly different at the $P < 0.01$ level. Many apparently complete active-capture sequences involving flapping of swimming feet and second maxillae were observed for *Chlamydomonas* sp. and *C. proteus* without any cell being visible: in 48% and 72% of the sequences, respectively, no cell was seen. Only one flapping sequence (without a target being seen) was ever observed for *C oblonga* on any film. Because of the enormous opportunities for contact between *D. sicilis* and *C. oblonga* resulting from the high concentration of cells and the possibility of fecal debris in the algal suspension that might have elicited an active capture response (*see below*), we concluded that *C. oblonga* was never captured actively.

Results in Tables 1 and 3 suggest that algal size is the dominant factor explaining active capture intensity (as revealed by the percentage of captures that are active), but that algal concentration may play a significant secondary role. For example, the active capture intensity for *Chlamydomonas* sp. at 3 mm^3 $liter^{-1}$ is significantly greater than that for *C. proteus* at 1 and 3 mm^3 $liter^{-1}$, but not at 0.3 mm^3 $liter^{-1}$. No significant differences were observed with different concentrations of *C. proteus* (Table 3), but active capture intensity of *C. proteus* at the lowest concentration was significantly higher than that for the combined results at the two higher concentrations. Possibly satiation is the explanation for the decrease in active capture intensity with increasing algal concentration, since 1 mm^3 $liter^{-1}$ of *Chlamydomonas* sp. or *C. proteus* is satiating (Vanderploeg et al. 1984). In this situation, the animal would ignore—that is, passively reject (Strickler 1984)—particles within the normal striking range of a hungry animal.

A primary function of the maxillipeds is to direct large particles from the flow field beneath the animal toward the second max-

Table 3. Summary of possible comparisons from Table 1 of percentage of captures that are active captures for different algal species and concentrations. The algae, abbreviated by their initials, are ordered in decreasing size and, within species, by increasing concentration. Concentration values (mm^3 $liter^{-1}$) are given in parentheses following the initials. Each matrix element shows the significance of a one-tailed χ^2 test to determine if the proportion of active captures observed for the experimental conditions indicated by the row label is significantly greater than that for the column label. NS indicates a nonsignificant ($P > 0.05$) difference.

	C.s. (3)	*C.p.* (0.3)	*C.p.* (1)	*C.p.* (3)	*C.o.* (0.8)	*C.o.* (3)
C.s. (1)	NS	NS	0.05	NS	0.05	0.01
	C.s. (3)	NS	0.05	0.05	0.01	0.01
		C.p. (0.3)	NS	NS	0.05	0.01
			C.p. (1)	NS	NS	0.05
				C.p. (3)	NS	0.05
					C.o. (0.8)	NS

illae; without the maxillipeds, selectivity for large particles would be considerably lower. The percentage of active captures aided by the maxilliped (combined for all concentrations in Table 1) was 69% for *Chlamydomonas* sp., significantly greater (χ^2 test, $P < 0.05$) than the 35% for *C. proteus*. If maxilliped-aided captures were subtracted from the total of active captures, the percentage of active captures (averaged over all concentrations) for *Chlamydomonas* sp. and *C. proteus* would be 15 and 13%, quite different from the 36 and 18% with the maxilliped-aided captures included.

Rejection of algae—The rejection of captured algae is of interest because it provides insight into individual as opposed to group handling (sensu Paffenhöfer et al. 1982; Price et al. 1983) of cells. Such observations also provide insight into the effects of algal concentration on selectivity for different algae. Rejections were easily identified by characteristic mouthpart motions in marine copepods (Koehl and Strickler 1981; Price et al. 1983) with subsequent loss of the captured algae. In our experiments *Chlamydomonas* sp. was always rejected individually, whereas *C. proteus* and *C. oblonga* were often rejected as groups (Table 4). Thus, not only is *Chlamydomonas* sp. captured actively as one cell at a time, but it is rejected in the same manner. This implies, as Paffenhöfer et al. (1982) were able to observe directly with *E. pileatus*, that a number of small cells are accumulated near the mouth before being ingested.

The rejection rate of captured algae of all three species was highest at 3 mm^3 $liter^{-1}$, well above the concentration required to satiate the feeding response (Vanderploeg et al. 1984). The proportion of captured cells of *C. oblonga* and *C. proteus* rejected was significantly greater ($P < 0.01$) at 3 mm^3 $liter^{-1}$ than at lower concentrations (results for *Chlamydomonas* sp. were not significant). Actively captured as well as passively captured cells were rejected. It might be argued that for *C. proteus*, the smaller actively captured alga, a passively captured cell could have slipped in between the active capture and the rejection. Even so, active captures of algae just before rejections may imply that even satiated copepods use active capture. Another possible explanation for these results is that the 2.5-h preconditioning period in the 3-mm^3 $liter^{-1}$ experiments was not long enough for the animals to adapt to the taste of a different suspension of the same alga, despite all our precautions to ensure identical physiological conditions (*see methods*). That taste was not the factor is also suggested by the rejection of algae at lower concentrations, to which *D. sicilis* was preconditioned for 1 d.

Capture and rejection of large targets—The algal suspensions, in addition to individual cells of *Chlamydomonas*, also contained some larger particles that were captured by *D. sicilis* (Table 5). A small percentage of the *C. proteus* and *Chlamydomonas* sp. cells were found in palmelloid clusters. Fecal pellets and other debris were also occasionally present. *Diaptomus sicilis* usually actively captured fecal pellets and debris (probably of fecal origin) and then rejected them from near the mouth area. In

Table 4. Number of algae rejected (rej.) per rejection event and probability (Pr.) of rejection as it relates to algal capture (cap.) mode and concentration.

Algal concn (mm^3 $liter^{-1}$) and treatment	Cells rej. (No.)	Cells rej./cells cap.	Cells/rej.		Pr. rejection event following	
			Mean	Range	passive capture	active capture
Chlamydomonas sp.						
$1 \xrightarrow{1\ d}$ film	4	0.160	1	1	0.118	0.125
$0.3\text{–}1 \xrightarrow{1\ d} 3 \xrightarrow{2.5\ h}$ film	4	0.364	1	1	0.333	0.400
C. proteus						
$0.3 \xrightarrow{1\ d}$ film	2	0.063	1	1	0.087	0
$1 \xrightarrow{1\ d}$ film	0	0	—	—	0	0
$0.3\text{–}0.5 \xrightarrow{1\ d} 3 \xrightarrow{2.5\ h}$ film	26	0.743	1.73	1–6	0.387	0.400
C. oblonga						
$0.8 \xrightarrow{1\ d}$ film	0	0	0	0	0	—
$0.5 \xrightarrow{1\ d} 3 \xrightarrow{2.5\ h}$ film	13	0.619	1.62	1–3	0.381	—

one case, the end of a fecal pellet which was intact before capture was torn off at the time of rejection, suggesting that the animal rejected it after biting into it. Algal clusters, whether captured actively or passively, were less likely to be rejected: the 25% rejection rate (Table 5) of the clusters (captured either passively or actively) was significantly lower (χ^2 test, $P < 0.01$) than the 75% rejection rate of actively captured fecal pellets or debris and significantly lower ($P < 0.05$) than the 73% rejection of either actively or passively captured fecal pellets or debris. This suggests that fecal pellets and other organic debris give off appropriate signals—probably olfactory cues or disturbances in the flow field (Koehl 1981; Strickler 1984)—for active capture but not proper gustatory signals for ingestion. Thus it appears that *Diaptomus* can avoid ingesting fecal pellets and other large detritus. Ingestion of small detritus and inert particles is probably not usually avoided because great quantities of calcite crystals are found in the fecal pellets of *Diaptomus* during calcite whitings (Vanderploeg 1981).

Ecological implications: A general discussion

Mode switching and invariant selectivity—An important difference between *D. sicilis* and the marine copepods *Paracalanus* sp. and *E. pileatus* is that the second maxillae of *D. sicilis* continually oscillated during feeding at all concentrations of all three *Chlamydomonas* spp., whereas the marine copepods did not oscillate their second maxillae in monocultures of large (≥ 12 μm) algae (Price et al. 1983; Paffenhöfer 1984*a*). Although water does flow between the second maxillae when they are still, the flow is thought to increase when they oscillate (Price et al. 1983), so that the capture rate of small cells increases when the marine copepods turn on this "enhanced" mode of passive capture. Since in *D. sicilis* this enhanced passive-capture mode is always turned on during feeding, the rate at which water flows between the second maxillae should remain constant, and this flow rate relative to the rate at which water flows past the animal should remain constant as well. The flow rate between the left and right second maxillae is proportional to the clearance rate (ml d^{-1}) of passively collected (small) cells, and the flow rate of water past the animal is proportional to the clearance rate for encounter of actively captured cells. Consequently selectivity, W' (Vanderploeg and Scavia 1979), for small cells [(clearance rate on small cells)/(clearance rate on large cells)] would in theory be expected to change for the marine copepods as proportions of large and small cells vary but not for *D. sicilis*. Reasoning

like this led Vanderploeg (1981) to predict from the relatively invariant pattern of particle-size selection by *D. sicilis* on lake seston that active and passive modes of feeding must operate simultaneously at all times. The filmed observations verify this hypothesis. Later work showed that W' for *C. oblonga* relative to *Chlamydomonas* sp. did not change over two orders of magnitude of relative proportions of biomass of small to large cells and a broad range of total concentration of the two algae (Vanderploeg et al. 1984). The lack of flexibility in *D. sicilis* in turning off its enhanced passive-capture mode is certainly part of the reason for its invariant selectivity.

Further discussion of the relevance of our cinematographic observations to selectivity is aided by a simple model. Imagine, as Alcaraz et al. (1980) did, a plane perpendicular to the long axis of the body of the copepod, cutting the axis at the level of the second maxillae. A contour line that bounds the second maxillae represents the region within which an alga—if not too small to slip through the "filter" apparatus—will be captured passively (if not first captured actively). The region bounded by this contour line and the next one out represents a region of high probability of active capture, if the alga is large enough to be actively captured and the copepod is hungry. The region of active capture is larger than that of passive because copepods sensing an oncoming alga will turn toward it and capture it (Strickler 1982). The next region outward will represent a lower probability of capture. As the algae become larger, the contour lines for active capture would be expected to extend further out. Cinematographic evidence for this is the higher proportion of maxilliped-aided captures observed for *Chlamydomonas* sp. than for *C. proteus*. These probability contours may be converted—at least abstractly—into an equivalent cross-sectional area from which a copepod will capture all algae of a given size that flow through. Moreover, it is helpful to think of the copepod as having an effective encounter area within which a *hungry* animal will capture all algae of a given size as they flow through.

When speaking of invariant selectivity, it is important to remember that we are referring to actual ingestions by the animal that are the end result of a number of steps, some of which involve sensory processes. Imagine selection in mixtures of a large alga and a small, passively collected alga. The simplest way that invariant selection will be maintained is if the conditional probability of ingesting the large algae subsequent to their entry into the effective encounter area for active capture equals the conditional probability of ingestion of the small algae after passive capture. The only way these conditional probabilities can be equal is if the conditional probability of rejecting or not sensing large algae after their entry into the effective encounter area equals the conditional probability of rejecting passively captured algae. Rejection of algae for the active mode can be passive (ignoring algae in the effective encounter area: sensu Strickler 1984) or active (involving rejection motions of the second maxillae) after capture. In contrast, rejections of passively collected algae must be active. We implicitly assume that *Diaptomus* spp. cannot change the properties of their "filters" since they do not have muscles in the setae of the second maxillae (Friedman and Strickler 1975) to make these adjustments.

The ratio of active to passive captures decreased as *C. proteus* concentration increased (Table 1). It would be tempting to conclude that this decrease represented an increasing sensitivity of the sensors for ac-

Table 5. Capture and rejection of *Chlamydomonas* clusters, fecal pellets and debris, and other large objects. Algal concentration was usually 0.3 or 1 mm^3 $liter^{-1}$; average algal concentrations in experiments having captures of algal clusters and those having captures of fecal pellets and debris were 1.1 and 0.7 mm^3 $liter^{-1}$.

Object	Dimensions (μm)	No. of particles	Active captures (%)	Active and passive captures rejected (%)	Active captures rejected (%)
Algal clusters	12–50*	8	38	25	33
Fecal pellets and debris	14–61*	11	73	73	75
Fiber (filter paper)	6 × 90	1	0	100	—

* Range of longest dimensions of objects.

Table 6. Equivalent spherical diameters (ESD) of actively and passively collected algae, clearance rates (F_{pref}) on the preferred (large) algae expressed per unit of C, and the selectivity coefficient W' (Vanderploeg and Scavia 1979) for the passively collected algae ($W' = F_p/F_{pref}$, where F_p is the clearance rate of the passively collected alga) for three species of freshwater and marine calanoid copepods (Paffenhöfer 1984*b*; Vanderploeg et al. 1984). All clearance rates were calculated from algal concentrations determined with an inverted microscope. Clearance rates of the *D. sicilis* females were determined at 10°C and for the marine copepods (CV and/or females) at 20°C.

	C content (μg)	Metasome length (mm)	ESD of actively collected algae (μm)*	ESD of only passively collected algae (μm)	Preferred alga ESD (μm)	Preferred alga F_{pref} C^{-1} (ml d^{-1} μg^{-1})	Passively collected alga ESD (μm)	Passively collected alga W'
Diaptomus sicilis	7.5	1.2	6–35†	≤4	12	3.2	4	0.34
Paracalanus sp.	3.9	0.7	10–~35‡	<6–8	13	20	6	0.10
Eucalanus pileatus	36	1.9	10–~70§	<6–8	13	7.8	6	0.04

* Upper limit is given for the diameter of a spherical alga that can be swallowed. Algae of greater ESDs can be ingested if they have an elongated shape, because they are placed in the mouth lengthwise before chewing and ingestion (Paffenhöfer and Knowles 1978).
† Upper limit determined from largest *Stephanodiscus* spp. found in fecal pellets (Vanderploeg 1981).
‡ Paffenhöfer (unpubl. data).
§ Upper limit is diameter (width) of *Rhizosolenia* colonies that can be ingested (Paffenhöfer and Knowles 1978).

tive capture at low concentrations of algae. Since such increased sensitivity could not be balanced by an increased capture efficiency of the passive mode, it would lead to variable selection with changes in concentration of our hypothetical algal mixture. An alternative explanation is that, as hunger decreased with increasing food concentration, an increasing proportion of *C. proteus* cells was passively rejected. This latter explanation is consistent with the invariant selectivity observed for mixtures of *Chlamydomonas* sp. and *C. oblonga* (Vanderploeg et al. 1984).

The shape of the selectivity vs. particle-size curve—Price et al. (1983) concluded from their cinematographic study of *E. pileatus* and *Paracalanus* sp. that the sharp increase in selectivity observed above 12 μm for *Diaptomus* spp. feeding on seston (Richman et al. 1980) and above 13–15 μm for *Calanus pacificus* feeding on cultured diatoms (Frost 1977) was caused by a sharp size threshold for individual detection and active capture of algae. The case cited for *Diaptomus* spp. was much more striking than that for *C. pacificus*. However, in another study with seston and with mixtures of *Chlamydomonas* spp., *D. sicilis* exhibited a gradual increase in selectivity with increasing particle size between 3 and 12 μm (Vanderploeg 1981).

In all these feeding studies a Coulter counter was used to measure algal concentration. Vanderploeg (1981) and Vanderploeg et al. (1984) argued that the results of Richman et al. (1980) were seriously biased by zooplankton-produced particles, a potential artifact in all Coulter-analyzed results. Another factor in their study that may have been important—a factor of potential importance in all studies with natural seston—was particle taste (Vanderploeg 1981; Vanderploeg et al. 1984). Seston is composed of both algae and nonliving particles; in our films, *D. sicilis* actively rejected fecal pellets and debris.

We believe that selectivity should show a smooth monotonic increase with increasing particle size in mixtures of "good-tasting" algae until a maximum is reached. This results from active selection, which would increase with increasing particle size to some maximum value, superimposed upon passive selection that would also increase to some maximum value, probably at a particle size smaller than that at which the maximum value for active selection occurred (e.g. Vanderploeg and Ondricek-Fallscheer 1982). Data on selectivity vs. particle size for mixtures of algae counted with the inverted microscope, which does not introduce the bias of zooplankton-produced particles, do show that selectivity increases smoothly with particle size until a maximum is reached. Bartram (1981) obtained such curves for *Acartia clausii* and *Paracalanus parvus*. A gradual increase is also

suggested for *D. sicilis* since a value of 0.34 for selectivity (W') of the passively collected *C. oblonga* relative to the value of 1.0 for the 12-μm *Chlamydomonas* sp. was obtained (Vanderploeg et al. 1984).

The cinematographic evidence for the smooth increase is in our filmed observations that *C. proteus,* the intermediate-sized alga, was captured actively at a lower rate than *Chlamydomonas* sp., the large alga. Price et al. (1983) based their conclusion on the observation that algae of 12-μm ESD were captured actively and algae of 6-μm ESD were not. Implicit in the idea of a threshold is that receptors would be triggered by a signal like a phycosphere of odor around an alga if it exceeded a certain size. We suggest that the size of the signal reaching the receptors could depend on the position of the alga relative to the receptors. As discussed above, we would expect the capture-probability contours to expand outward with algal size until some maximum is reached. This would result in a smooth increase in selectivity with algal size. Possibly, if *Paracalanus* sp. and *E. pileatus* were given an alga between 6 and 13 μm, they would capture it actively at a lower rate than the 13-μm cells.

Small particle specialization—The continual oscillation of the second maxillae of *D. sicilis* can be viewed as a specialization for capture of small particles, since it enhances flow of water between the second maxillae. Specialization of *D. sicilis* for small particle capture can also be inferred from its morphology and the current field around it. The large, anteriorly located swimming legs of *D. sicilis,* in contrast to the relatively smaller, posteriorly located swimming legs of *E. pileatus* (*see inset of Fig. 1*), seem to direct water into the mouthparts. Further evidence is the ability of *D. sicilis* to actively capture 6-μm cells, whereas the marine copepods *Paracalanus* sp. and *E. pileatus* do not (Table 6).

These inferences based on the cinematography are corroborated by the comparison of particle-size selection by *D. sicilis* with that of the two marine copepods (Table 6). Mean selectivity (W') for the small, passively collected alga (ESD = 4 μm) was 0.34 for *D. sicilis,* whereas corresponding values

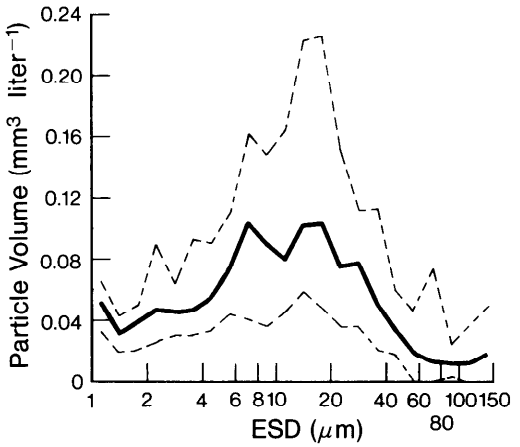

Fig. 5. Average particle-size spectrum (solid line) available to *Diaptomus sicilis* in offshore Lake Michigan during April–November. Dashed lines show maximum and minimum values. Results were calculated from 15 experiments (Vanderploeg 1981) conducted over a 2-yr period (1977–1978) at about monthly intervals.

for *E. pileatus* and *Paracalanus* sp. were 0.04 and 0.1 (Paffenhöfer 1984*b*: figs. 3 and 4) for the passively collected, 6-μm alga (Price et al. 1983). This difference cannot simply be attributed to the size of the copepods because *Paracalanus* sp. is even smaller than *D. sicilis* (Table 6) and because, as already noted, the morphological and behavioral specializations of *Diaptomus* are consistent with small particle capture.

Since *D. sicilis* is a relatively large copepod with mouthparts resembling those of other herbivorous diaptomids (e.g. drawings of Sars 1903; Storch and Pfisterer 1925; Gurney 1931; electron micrographs of Friedman 1980), it is probably reasonable to assume that relative to the marine copepods the genus *Diaptomus*—the most important group of herbivorous copepods in freshwater—may be regarded as small-particle specialists. This specialization is consistent with recent data suggesting that small particles contribute more to the particle-size spectra of lakes than to those of the ocean (Richman et al. 1980; Vanderploeg 1981; Sprules et al. 1983). Individual spectra (Richman et al. 1980; Vanderploeg 1981), as well as the average particle-size spectrum (Fig. 5), for Lake Michigan differ from both

temperate (Sheldon et al. 1972, 1977; Poulet 1974) and subtropical marine spectra (Sheldon et al. 1972, 1977; Paffenhöfer et al. 1980; Paffenhöfer 1983) in that marine spectra are often flat, and when they are not—as in temperate coastal environments or during upwellings in subtropical environments—particles >20–30 μm often dominate. The average Coulter-measured spectrum for Lake Michigan (Fig. 5) is very similar to the average obtained for algae in 26 Ontario lakes of varying trophy by Sprules et al. (1983), who counted the algae microscopically. We believe that it would be extremely useful to observe feeding mechanisms in other freshwater and marine copepods and classify them into different categories on the basis of their observed feeding mechanisms so that the development of adequate models of selectivity and feeding can be hastened (e.g. Vanderploeg et al. 1984).

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